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Genetic variation among mountain pine beetle subpopulations along an endemic to epidemic gradient across the north slope of the Uinta Mountains in Utah

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RESEARCH REPORT

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GENETIC VARIATION AMONG MOUNTAIN PINE BEETLE SUBPOPULATIONS ALONG AN ENDEMIC TO EPIDEMIC GRADIENT ACROSS THE NORTH SLOPE OF THE UINTA MOUNTAINS IN UTAH

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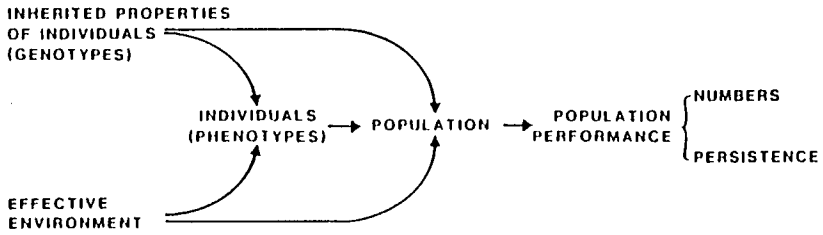
INTRODUCTION

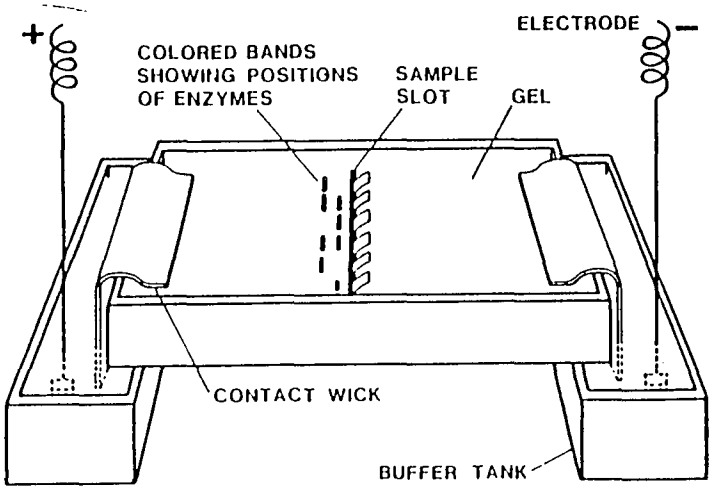
Periodic, naturally-occurring changes in insect numbers (outbreaks and population declines) cannot be simply explained by studying only the extrinsic or environmental factors (such as food supply or temperature) that affect the insects. We know, for example, that apparently favorable environmental conditions don't always lead to an outbreak. Some mountain pine beetle populations, in an area that seems favorable for an outbreak, stay at fairly low levels for several years while, in nearby areas, the density rises precipitously and an outbreak occurs.



LIFE SYSTEM

Changes in density of forest insect pest populations result from interactions between the environment and the intrinsic or genetic properties of the insects (see diagram above; Clark et al.'s 1967 "life system"). The genetic makeup of an insect population not only reflects a response to environmental changes, it is a feature that can directly alter its response to the environment. Genetic changes continually occur within insect species, both from place to place and time to time. This variation affects critical life processes, such as fecundity, the ability to withstand natural environmental stresses (a limited food supply, crowding, or temperature extremes, for example), and responses to human activity aimed at controlling these insects. A well-known example is differences in tolerance to insecticides among insect populations. This phenomenon is well-studied in agricultural insect pests. Forest defoliators, such as the Douglas-fir tussock moth and the western spruce budworm, also vary greatly in their response to insecticide application. These differences cannot be explained simply by the environmental conditions at the time of spray application. Genetic tests, using electrophoresis, have demonstrated that differences in response are inherited and constitute an intrinsic feature of these insects that must be considered when control strategies are being developed. Knowledge of the genetic constitution of a pest species is therefore an essential component in understanding the population dynamics of any important pest insect species.

One of the goals of the forest manager and the applied forest entomologist is to develop methods to predict density changes in local forest insect pest populations. Genetic data, acquired using electrophoresis, is proving of considerable value for such purposes. For example, information on the inherent levels of susceptibility to particular insecticides is now being incorporated into computer models for predicting response of forest defoliators to these chemicals.



Using this technique, a considerable body of research has accumulated in the past 10 years that directly relates to our understanding of the population dynamics of insects. Two types of genetic change have been specifically associated with density fluctuations; both have potential or actual value for predicting such fluctuations. The first is a change in genetic diversity. Some theoretical and experimental work suggests that genetic diversity increases during a population increase, as relaxed environmental selection (lack of stress) permits a wider range of genotypes to survive. According to this scheme, genetic variation decreases when selection pressures increase and the less fit genotypes perish.

Other evidence suggests that, in some plant and animal groups, the reverse may occur. Stress upon a population may result in increased genetic diversity. Field workers have observed, for example, greater color variation among Douglas-fir tussock moth larvae during a population crash. And our experiments (Stock and Amman 1984, in press, Banff paper) show that mountain pine beetle raised in thin-phloem lodgepole pine (stressful conditions of crowding and minimal food supply) are more genetically diverse than beetles raised in thick-phloem lodgepole pine.

The other type of genetic change associated with density fluctuations is a shift in allele frequencies at one or more gene loci. In the Douglas-fir tussock moth, for example, allele frequencies at an esterase locus fluctuate

with population density. Of particular interest is that these changes can be detected, using electrophoresis, before density changes can be detected by more traditional methods in the field or laboratory.

The objective of the study described here was to identify specific genetic attributes of endemic and epidemic mountain pine beetle populations and to determine to what extent these attributes are reliable indicators of population phase. To achieve this goal, we obtained samples of mountain pine beetle from a series of locations within the large and relatively contiguous outbreak along the north slope of the Unita Mountains in northeast Utah. These samples were chosen to represent (1) a range of naturally-occurring density levels or "population phases" from low level (endemic) through outbreak (epidemic) to post-outbreak, and (2) sites for which data had been obtained for earlier years and/or where two generations of beetles could be obtained, by appropriate rearing methods, to permit year-to-year genetic comparisons.

Using electrophoresis, we attempted to answer the following questions:

1) Does any consistent change in genetic diversity--associated with density level--occur over space (from site to site) or over time (from year to year)??

Our hypothesis was that, as populations build toward a peak density in an outbreak, a decrease in genetic diversity would be observed. Conversely, as populations peak and decline, levels of genetic diversity would increase. This hypothesis is based on our observation that mountain pine beetles reared in thin phloem are more genetically diverse than those reared in thick phloem. If this hypothesis is correct, shifts in genetic diversity might reflect levels of stress being encountered by a particular "subpopulation" and might therefore be used to help predict trends in numbers in that population in subsequent years.

2) Are any shifts in allele frequencies, either over space or time, associated with density differences??

Our hypothesis here was that examination of allele frequencies at polymorphic gene loci (that is, loci producing a number of different gene products) would reveal shifts that would reflect density differences. This hypothesis is based on a large body of research (ours and many, many others) that demonstrates a direct relationship between electrophoretically detectible genetic changes and density shifts.

METHODS

Mountain pine beetles were collected from 8 sites along the north slope of the Uinta Mts. during summer 1982. At each site, lodgepole pine billets were cut from one or more thick-phloem lodgepole pine trees. At the Ogden laboratory, emerging adults were collected and mailed in petri dishes containing sawdust to the University of Idaho laboratory. There beetles were sorted and subjected to electrophoretic analysis. At some sites, billets collected later in the summer contained larvae that were cold-stored until November. Adults emerging from these billets in late November and early December 1982 were collected and used to represent the 1983 generation that would emerge naturally in the field the following summer (1983).

Methods for electrophoresis of bark beetles have been described by Stock and Amman (1980) and Higby and Stock (1982). Electrophoresis was carried out on homogenates of individual beetles inserted in slots in a 13% starch gel using a discontinuous buffer system. Gels were electrophoresed at 75 mA for 1-4 hours, then sliced horizontally and each slice stained separately for a single enzyme type. Variation of enzyme products of a diversity of gene types was recorded and compared among groups.

For the preliminary analyses described here, genotype frequencies were converted into allele frequencies for each group. In addition, heterozygosity (h, Nei 1975) at individual loci and average heterozygosity (H) were calculated to estimate and compare levels of genetic diversity among groups.

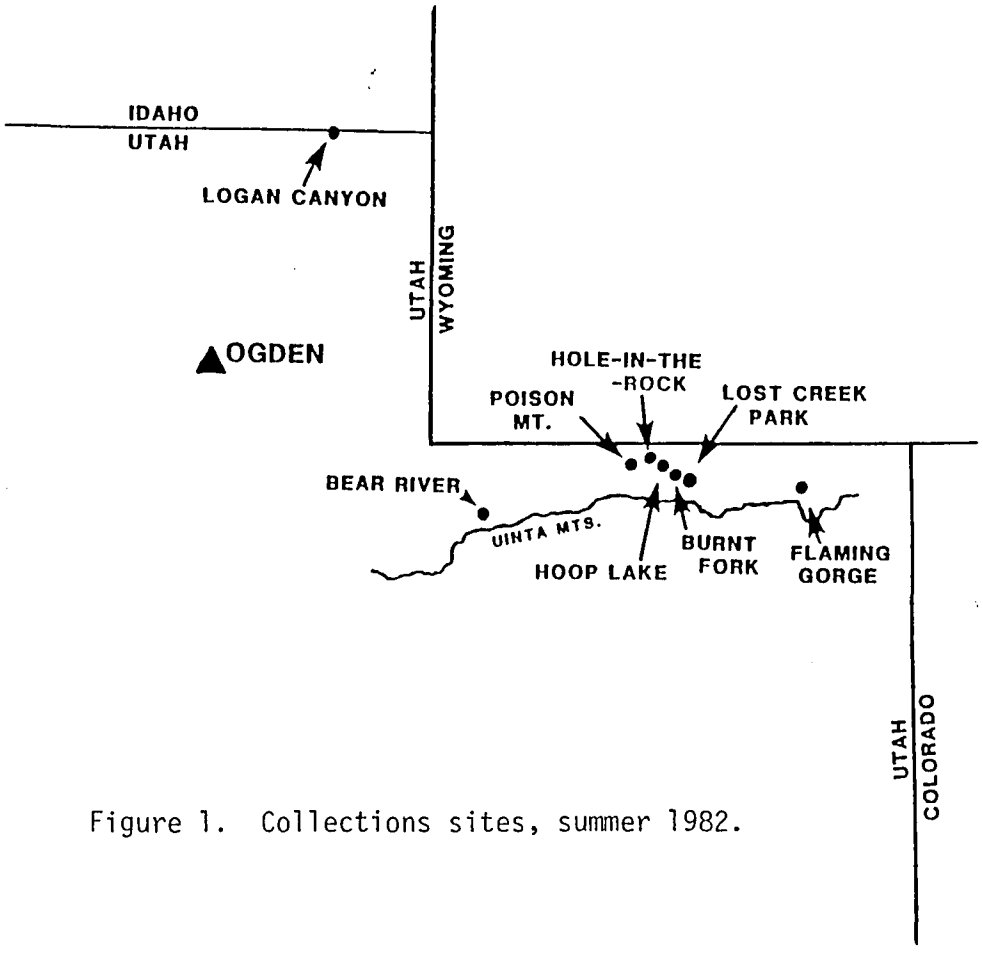


Figure 1. Collections sites, summer 1982.

RESULTS

Collection sites in the Wasatch and Ashley National Forests in NE Utah are shown in Figure 1 (map). Infestation categories of the sites are based on a general overall impression of the number of trees infested per unit area and the infestation pattern, rather than specific measures such as mean attack density or emergence per square foot.

Endemic: Poison Mt. and Hole-in-the-Rock sites. Infested trees widely scattered (approximately 1 per 100 acres) rather than grouped, with short infested tree lengths (usually less than 10 feet).

Building: Burnt Fork and Hoop Lake sites. Infested trees more numerous than above (3-20 per 100 acres); some tendency toward grouping, though generally less than 5 trees in an immediate group; infested tree lengths usually greater than 10 feet.

Static: Logan Canyon site. Similar to the "building" category, with the exception that there is little change in the number of trees infested or infested length from year to year.

Outbreak: Lost Creek Park and Flaming Gorge sites. Number of infested trees more than in "endemic" and "building" categories; trees tend to be grouped (6 or more per center); infested length generally greater than 15 feet.

Post-outbreak: Bear River site. Virtually all large diameter trees have been killed; current infestation mostly in smaller diameter trees; infested lengths generally shorter than outbreak status.

Samples representing 1982 adults were obtained from Poison Mt., Hole-in-the-Rock, Hoop Lake, Flaming Gorge, Lost Creek Park, Logan Canyon and Bear River. Samples representing 1983 were also obtained from Hoop Lake, Lost Creek Park, and Logan Canyon. Only 1983 adults were obtained from Burnt Fork.

Data were obtained on 7 polymorphic loci (EST1, AAT1, PEP-LA, PEP-GL, PGI, AcP, and LAP2) and 7 monomorphic loci (ME, MDH1, MDH2, AGP1, AGP2, IDH, and MPI). Polymorphic loci were defined as those with a frequency of the common allele less than .95 in at least one group. Allele frequencies, heterozygosity, and average heterozygosity are shown in Table 1. For additional year-to-year comparisons, data on these loci from Stock, Amman, and Higby (in press) are also shown for 1980 beetles from Hoop Lake, Flaming Gorge, Logan Canyon, Bear River, and Dubois (Wyoming). Previously unreported data from 1979 beetles from Hoop Lake, Flaming Gorge, Logan Canyon, Bear River, and Dubois are also shown.

Table 1. Allele frequencies at 14 gene loci (7 polymorphic, 7 monomorphic) in 8 Utah mountain pine beetle populations. Data also shown for beetles from one additional site (Dubois, Montana; 1979 data previously unreported elsewhere, 1980 data reported in Stock, Amman, and Higby 1984). Heterozygosity (h) for each polymorphic locus and average heterozygosity (H) for (1) the 5 polymorphic loci (EST1, AAT1, PEP-GL, PGI, and LAP2) for which data are available for all groups, (2) 7 polymorphic loci for groups for which data were also obtained on PEP-LA and AcP, and (3) a combination of the 5 common polymorphic loci and the 7 monomorphic loci are provided to permit comparison of diversity levels among and within groups.

		Endemic →		Building →				Outbreak →					Static →				Post-outbreak			Dubois	
		Poison Mt.	Hole-in-the-Rock	Burnt Fork	Hoop Lake				Flaming Gorge			Lost Creek Park		Logan Canyon				Bear River			
Locus	Allele	1982	1982	1983	1979	1980	1982	1983	1979	1980	1982	1982	1983	1979	1980	1982	1983	1979	1980	1982	1979	1980
EST1	1	.08	.04	.02	.02	.05	.03	.04	-	.01	.04	.01	.01	.02	.02	.05	.03	.03	.02	.01	.05	.02
	2	.44	.43	.39	.44	.47	.42	.43	.25	.40	.43	.49	.55	.40	.29	.26	.33	.30	.36	.33	.41	.33
	3	.20	.23	.25	.20	.22	.20	.24	.20	.24	.22	.16	.15	.25	.31	.22	.26	.33	.21	.30	.13	.31
	4	.06	.12	.08	.09	.03	.14	.09	.25	.12	.04	.09	.08	.09	.09	.06	.11	.10	.11	.08	.16	.08
	5	.22	.17	.21	.25	.23	.22	.20	.24	.23	.26	.25	.21	.24	.29	.40	.25	.23	.29	.27	.25	.26
	6	-	-	-	-	-	-	-	.04	.01	-	-		.01	.01	-	-	.01	.01	-	.01	-
	N	56	190	66	114	97	55	207	79	868	59	45	49	618	100	31	107	352	94	95	128	97
	h	.71	.72	.73	.69	.67	.71	.71	.78	.71	.70	.66	.62	.71	.73	.72	.75	.74	.73	.72	.72	.72
AAT1	0	-	-	-	-	-	-	.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	1	.11	.03	.02	-	-	.12	.06	-	-	-	.04	.03	-	-	-	.02	-	-	.01	-	-
	2	.60	.65	.63	.64	.66	.67	.60	.48	.62	.52	.57	.67	.66	.66	.60	.70	.64	.65	.59	.66	.66
	3	.29	.32	.35	.36	.34	.21	.33	.52	.38	.48	.39	.30	.34	.34	.40	.27	.36	.34	.39	.34	.34
	N	60	170	53	107	60	63	199	48	706	24	42	50	378	38	25	166	298	87	86	156	62
	h	.54	.47	.48	.46	.45	.49	.53	.50	.47	.50	.52	.46	.45	.45	.48	.44	.46	.46	.50	.45	.45
PEP-LA (data missing for some years)	1	.03	.02	.01	-	-	-	.02	-	-	-	.03	.07	-	-	-	.01	-	-	.05	-	-
	2	.77	.84	.96	-	-	.89	.88	-	-	.93	.82	.81	-	-	1.0	.96	-	-	.81	-	-
	3	.20	.14	.03	-	-	.11	.10	-	-	.07	.15	.12	-	-	-	.03	-	-	.14	-	-
	N	39	155	56			50	176			21	31	54			14	150			69		
	h	.37	.27	.08			.20	.22			.13	.30	.32			0	.08			.32		
PEP-GL	1	.03	.01	-	-	-	-	.01	-	-	-	-	.01	-	-	-	.01	-	-	.01	-	-
	2	.94	.94	.92	.90	.88	.93	.91	.98	.97	.92	.80	.80	.99	.98	1.0	.97	.92	.95	.86	1.0	.96
	3	.03	.05	.08	.10	.12	.07	.08	.02	.03	.08	.20	.19	.01	.02	-	.02	.08	.05	.13	-	.04
	N	60	193	101	106	100	62	211	82	864	18	35	52	541	96	33	166	344	94	98	130	99
	h	.12	.11	.15	.18	.21	.13	.16	.04	.06	.15	.32	.32	.02	.04	0	.06	.15	.09	.24	0	.08
PGI	1	.02	.02	.01	-	-	.01	.01	-	-	.01	.07	.01	-	-	.07	.02	-	-	.02	-	-
	2	.90	.95	.98	1.0	1.0	.94	.98	.99	.99	.98	.91	.94	.99	1.0	.93	.95	1.0	1.0	.82	1.0	1.0
	3	.08	.03	.01	-	-	.05	.01	.01	.01	.01	.02	.05	.01	-	-	.03	-	-	.16	-	-
	N	67	225	79	116	100	54	223	72	887	65	45	45	541	100	20	201	327	100	100	102	90
	h	.18	.10	.04	0	0	.11	.04	.02	.02	.04	.17	.11	.02	0	.13	.10	0	0	.30	0	0
AcP (data missing for some years)	0	-	.005	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.01	-	-
	1	.10	.09	.15	-	-	.05	.20	-	-	.01	.12	.06	-	-	.36	.10	-	-	.26	-	-
	2	.55	.60	.55	-	-	.59	.44	-	-	.38	.75	.67	-	-	.50	.55	-	-	.41	-	-
	3	.26	.31	.29	-	-	.36	.36	-	-	.61	.13	.28	-	-	.14	.35	-	-	.32	-	-
	N	19	98	29			35	94			13	0	16			11	73			49		
	h	.62	.54	.59			.52	.64			.48	.41	.47			.60	.56			.66		
LAP2	0	.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.01	-	-
	1	.28	.18	.03	.05	.02	.13	.06	.23	.05	.17	.17	.04	.03	.01	.20	.08	.05	.03	.23	.05	.08
	2	.61	.67	.79	.64	.61	.73	.79	.41	.69	.75	.58	.45	.54	.57	.50	.79	.60	.46	.66	.50	.51
	3	-	.14	.18	.31	.38	.14	.15	.36	.26	.08	.25	.50	.42	.41	.25	.12	.35	.51	.10	.45	.41
	N	9	78	28	48	90	26	96	37	586	6	18	11	145	88	10	62	176	61	35	44	80
	h	.55	.50	.34	.49	.48	.43	.35	.65	.45	.40	.57	.55	.53	.51	.64	.35	.51	.53	.50	.54	.56
ME	1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
MDH1	1	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"
MDH2	1	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"
AGP1	1	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"
AGP2	1	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"
IDH	1	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"
MPI	1	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"	"
H (poly minus AcP & PEPLA)		.42	.38	.35	.36	.36	.37	.36	.40	.34	.36	.45	.41	.35	.35	.39	.34	.37	.36	.45	.34	.36
H (all poly)		.44	.39	.34	-	-	.37	.38	-	-	.34	.42	.41	-	-	.37	.33	-	-	.46	-	-
H (5 poly + 7 mono)		.17	.16	.14	.15	.15	.16	.15	.17	.14	.15	.19	.17	.14	.14	.16	.14	.15	.15	.19	.11	.15

Question #1: Does any consistent change in genetic diversity--associated with density level--occur over space (from site to site) or over time (from year to year)??

Site-to-site comparisons of genetic diversity are shown in Table 2 and Figure 2. These data clearly support our hypothesis that genetic diversity decreases during the building phase of an outbreak and then rises during stressful conditions of peak outbreak and post outbreak phases.

Shifts in genetic diversity over time at single sites are summarized in Figure 3. Inferences from this table are as follows:

Bear River beetles show a marked increase in genetic diversity from 1980 to 1982. This reflects the highly stressful environmental conditions (i.e., limited food supply, crowding, etc.) now imposed upon this population.

Lost Creek Park beetles have exhibited a reduction in genetic diversity from 1982 to 1983. This may indicate that the population is not unduly stressed and that the outbreak is likely to continue for some time into the future.

Logan Canyon beetles show an increase in genetic diversity from 1979 to 1982, but a marked decrease from 1982 to 1983. This suggests that the population is not under as much stress as it was before and could become a more active outbreak in the future. The same trend is apparent in the "building" Hoop Lake population.

Flaming Gorge beetles showed a marked drop in genetic diversity from 1979 to 1980. This would be the expected pattern in an unstressed outbreak situation. The slight increase in genetic diversity in these beetles from 1980 to 1982 indicates that conditions are no longer as favorable as they were before and that the outbreak in this area may be close to achieving a peak in numbers.

Question #2: Are any shifts in allele frequency, either over space or time, associated with density differences?

Allele frequencies from year to year are summarized in Table 3. The notations on this table should perhaps be compared to Figure 3. Similar inferences can be obtained from both. For example:

The condition of the Hoop Lake population seems to have undergone a shift from 1980 to 1982.

Allele frequencies in the Flaming Gorge population seem to generally follow a linear trend from 1979 to 1982, but there is some indication (at the AAT1 and the LAP2 loci) that a shift of some sort occurred in 1980. This shift is more clearly apparent in Figure 3.

Lost Creek Park beetles show a clear shift in gene frequencies from 1982 to 1983. This shift results in the decrease in genetic diversity

seen in Figure 3.

The most obvious changes in allele frequency are seen in the Logan Canyon beetles; 1982 appears to signal a reversal of genetic trends occurring in 1979 and 1980. This reversal is also clearly apparent in Figure 3.

The major differences, seen in Table 3, for the Bear River population are a shift in genetic condition in 1980 and a greatly increased level of genetic diversity in 1982. See, for example, the AAT1 and the PGI loci; two additional alleles are apparent in both in 1982.

The question now is: Which, if any, of the alleles circled in Table 3 might be useful as indicators of density changes? In an attempt to answer this question, we must look at frequencies of these alleles from another perspective--space or site-to-site comparisons (Table 4). Those alleles that seem to change from year to year in several populations shown in Table 3 (EST1-alleles 2 and 4, AAT1-alleles 2 and 3, and LAP2-alleles 1, 2, and 3) are starred in Table 4. No association is apparent between density and frequency at any of these alleles.

CONCLUSIONS

Genetic diversity, either of individual polymorphic loci or over all loci, is directly related to environmental stress encountered by mountain pine beetle populations. Shifts in genetic diversity from year to year could be used to help predict numerical trends in subsequent years. Frequencies of the different alleles at polymorphic loci also give clues as to changes occurring in these populations, but no allele(s) can, at this point, be suggested as useful for association with density levels.

ACKNOWLEDGMENTS

We thank Carrie Lipe, Barbara Bentz, and Pam Higby for help with the laboratory work involved in this study.

Table 2. Heterozygosity (h) for 7 polymorphic gene loci and average heterozygosity (H) for these 7 loci and over all loci (including 7 monomorphic loci) for 7 Utah mountain pine beetle populations, 1982 collections only. Data excerpted from Table 1.

Locus	Poison Mt.	Hole-in-the-Rock	Burnt Fork	Hoop Lake	Flaming Gorge	Lost Creek	Bear River
EST	.71	.72	.73	.71	.70	.66	.72
AAT	.54	.47	.48	.49	.50	.52	.50
PEP-LA	.37	.27	.08	.20	.13	.30	.32
PEP-GL	.12	.11	.08	.13	.15	.32	.24
PGI	.18	.10	.04	.11	.04	.17	.30
AcP	.62	.54	.59	.52	.48	.41	.66
LAP2	.55	.50	.34	.43	.40	.57	.50
H (poly loci only)	.44	.39	.34	.37	.34	.42	.46
H (all loci)	.17	.16	.14	.16	.15	.19	.19

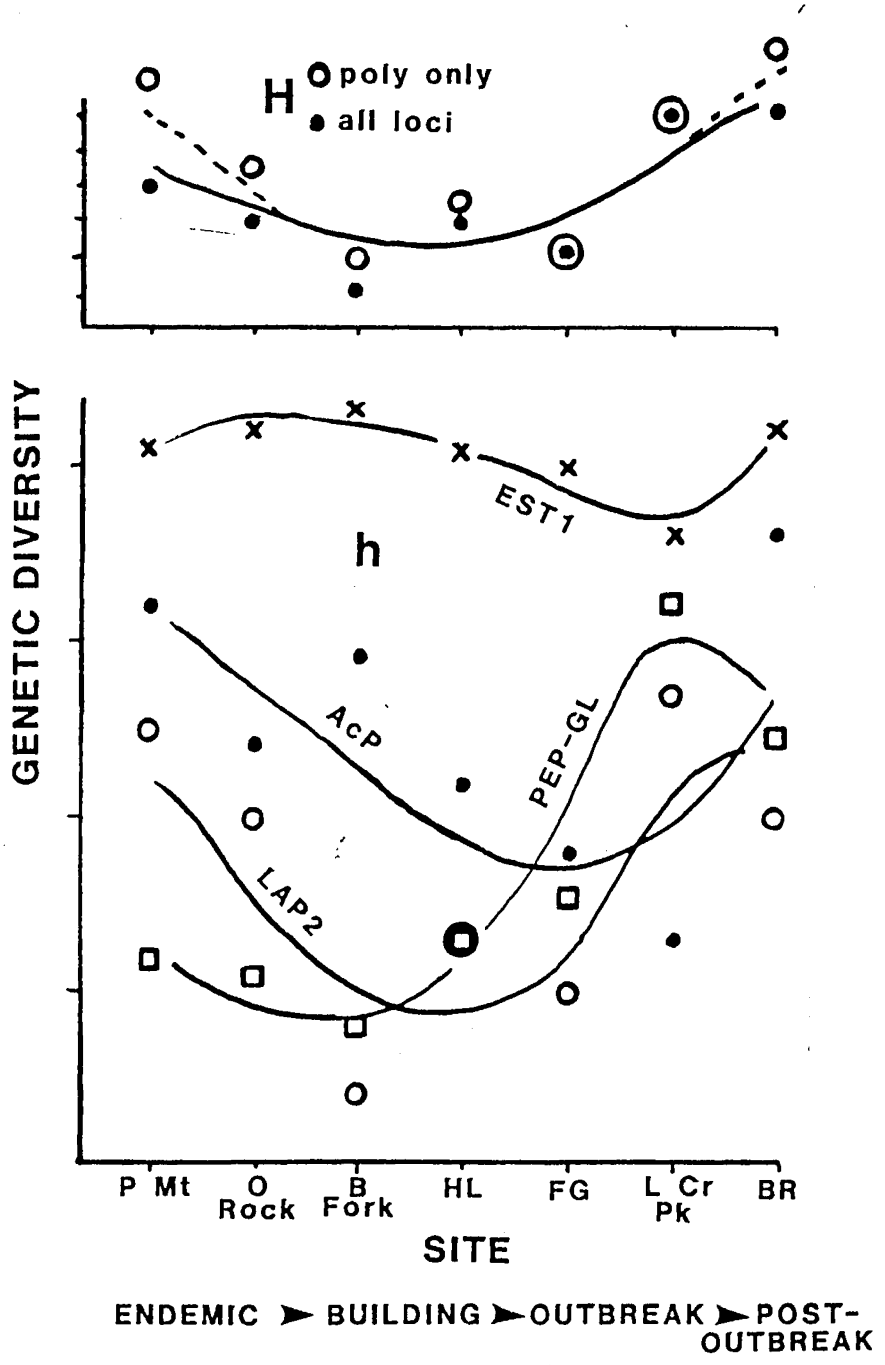


Figure 2. Shifts in genetic diversity associated with density differences from site to site. Lower diagram gives heterozygosity (h) for 4 of the polymorphic gene loci--EST1 (x), AcP (•) LAP2 (O), and PEP-GL (□). Upper diagram shows average heterozygosity (H) for the polymorphic loci only and over all loci. (Removing monomorphic loci from the calculation simply exaggerates the curve.) Data taken from Table 2.

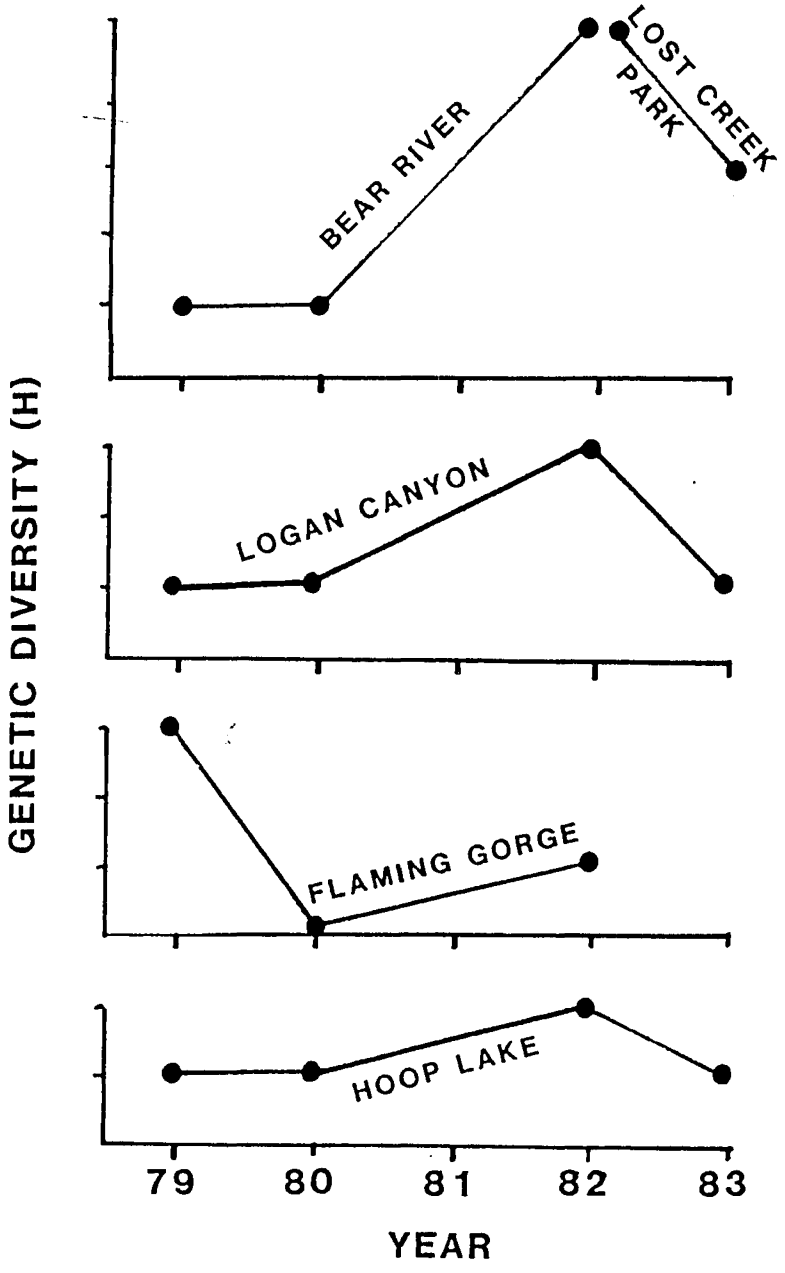


Figure 3. Shifts in genetic diversity (average heterozygosity or H for all loci, data taken from bottom of Table 1) from year to year at 5 sites. Shifts in diversity appear directly related to stress levels being encountered by these populations in the field.

Table 3. Allele frequencies at 5 polymorphic gene loci in mountain pine beetles from 6 locations obtained over a 2-5 year time span. Data from Table 1.

		Hoop Lake				Flaming Gorge			Lost Creek Pk.		Logan Canyon				Bear River			Dubois	
Locus	Allele	1979	1980	1982	1983	1979	1980	1982	1982	1983	1979	1980	1982	1983	1979	1980	1982	1979	1980
EST1	1	.02	.05	.03	.04	-	.01	.04	.01	.01	.02	.02	.05	.03	.03	.02	.01	.05	.02
	2	.44	.47	.42	.43 ↓	.25	.40	.43 ↑	.49	.55 ↑	.40	.29	.26	.33 ↘↗	.30	.36	.33 ↘	.41	.33 ↓
	3	.20	.22	.20	.24	.20	.24	.22	.16	.15	.25	.31	.22	.26	.33	.21	.30 ↗	.13	.31 ↑
	4	.09	.03	.14	.09 ↑	.25	.12	.04 ↓	.09	.08	.09	.09	.06	.11 ↗	.10	.11	.08	.16	.08 ↓
	5	.25	.23	.22	.20	.24	.23	.26	.25	.21	.24	.29	.40	.25 ↘	.23	.29	.27 ↘	.25	.26
	6	-	-	-	-	.04	.01	-	-	-	.01	.01	-	-	.01	.01	-	.01	-
AAT1	0	-	-	-	.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	1	-	-	.12	.06 ↓	-	-	-	.04	.03	-	-	-	.02	-	-	.01	-	-
	2	.64	.66	.67	.60 ↘↗	.48	.62	.52 ↘↗	.57	.67 ↑	.66	.66	.60	.70 ↘↗	.64	.65	.59	.66	.66
	3	.36	.34	.21	.33 ↗	.52	.38	.48 ↗	.39	.30 ↓	.34	.34	.40	.27 ↘	.36	.34	.39	.34	.34
	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.01	-	-
PEP-GL	1	-	-	-	.01	-	-	-	-	.01	-	-	-	.01	-	-	.01	-	-
	2	.90	.88	.93	.91	.98	.97	.92 ↓	.80	.80	.99	.98	1.0	.97 ↘	.92	.95	.86 ↘	1.0	.96
	3	.10	.12	.07	.08	.02	.03	.08 ↑	.20	.19	.01	.02	-	.02	.08	.05	.13 ↗	-	.04
PGI	1	-	-	.01	.01	-	-	.01	.07	.01	-	-	.07	.02 ↓	-	-	.02	-	-
	2	1.0	1.0	.94	.98 ↗	.99	.99	.98	.91	.94	.99	1.0	.93	.95 ↗	1.0	1.0	.82	1.0	1.0
	3	-	-	.05	.01 ↓	.01	.01	.01	.02	.05	.01	-	-	.03	-	-	.16	-	-
LAP2	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	.01	-	-
	1	.05	.02	.13	.06 ↘	.23	.05	.17 ↘	.17	.04 ↓	.03	.01	.20	.08 ↘	.05	.03	.26 ↑	.05	.08
	2	.64	.61	.73	.79 ↑	.41	.69	.75 ↑	.58	.45 ↓	.54	.57	.50	.79 ↗	.60	.46	.41 ↓	.50	.51
	3	.31	.38	.14	.15 ↓	.36	.26	.08 ↓	.25	.50 ↑	.42	.41	.25	.12 ↓	.35	.51	.32 ↘	.45	.41
	4	-	-	-	-	-	-	-	-	-	-	-	.05	-	-	-	-	-	-

Table 4. Allele frequencies at 7 polymorphic gene loci in 7 mountain pine beetle populations ranging from low density (endemic) to post-outbreak. Data excerpted from Table 1, 1982 data only (except for Burnt Fork).

		Endemic →		Building →	Outbreak →			Post-outbreak
Locus	Allele	Poison Mt.	Hole-in-the-Rock	Burnt Fork	Hoop Lake	Flaming Gorge	Lost Creek Park	Bear River
EST1	1	.08	.04	.02	.03	.04	.01	.01
	* 2	.44	.43	.39	.42	.43	.49	.33
	3	.20	.23	.25	.20	.22	.16	.30
	* 4	.06	.12	.08	.14	.04	.09	.08
	5	.22	.17	.21	.22	.26	.25	.27
	6	-	-	-	-	-	-	-
AAT1	0	-	-	-	-	-	-	-
	1	.11	.03	.02	.12	-	.04	.01
	* 2	.60	.65	.63	.67	.52	.57	.59
	* 3	.29	.32	.35	.21	.48	.39	.39
	4	-	-	-	-	-	-	.01
PEP-LA	1	.03	.02	.01	-	-	.03	.05
	2	.77	.84	.96	.89	.93	.82	.81
	3	.20	.14	.03	.11	.07	.15	.14
PEP-GL	1	.03	.01	-	-	-	-	.01
	2	.94	.94	.92	.93	.92	.80	.86
	3	.03	.05	.08	.07	.08	.20	.13
PGI	1	.02	.02	.01	.01	.01	.07	.02
	2	.90	.95	.98	.94	.98	.91	.82
	3	.08	.03	.01	.05	.01	.02	.16
AcP	0	-	.005	-	-	-	-	.01
	1	.10	.09	.15	.05	.01	.12	.26
	2	.55	.60	.55	.59	.38	.75	.41
	3	.26	.31	.29	.36	.61	.13	.32
LAP2	0	.05	-	-	-	-	-	.01
	* 1	.28	.18	.03	.13	.17	.17	.23
	* 2	.61	.67	.79	.73	.75	.58	.66
	* 3	-	.14	.18	.14	.08	.25	.10